MORPHOLOGY OF EUPTELEA AND COMPARISON WITH TROCHODENDRON

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With four plates

INTRODUCTION

In preceding papers (3, 4), we have discussed various fundamentally significant similarities between *Tetracentron* and *Trochodendron* which are indicative of relatively close genetic relationship. We shall now concern ourselves with a discussion of salient morphological features of *Euptelea* in an endeavor to determine whether this genus actually belongs in the family Trochodendraceae.

WOOD

The most significant difference between the wood of *Euptelea* and that of *Trochodendron* is the presence of well developed vessels in *Euptelea* and the absence of such structures in *Trochodendron*. The thin-walled, more or less angular vessels (*Fig. 1*) of *Euptelea* are numerous and diffusely distributed, but exhibit conspicuous size differences as between the early and late wood. The vessel members are relatively long with extensively overlapping ends and have scalariform perforation plates with numerous bars. The intervascular bordered pitting is transitional between scalariform and opposite-multiseriate, the former type tending to predominate in the smaller vessels, e.g. of young stems, the latter type in the larger vessels of older stems. The pitting between vessels and parenchyma is scalariform with transitions to opposite. The non-perforate tracheary elements are thick-walled fiber tracheids, having pits with reduced but conspicuous borders.

The wood parenchyma, which fluctuates from scanty to fairly abundant (*Fig. 1*), is distributed diffusely or in short tangentially oriented aggregates. As in *Trochodendron,* the wood parenchyma strands have a high ratio of obliquely oriented partitions. The rays in the outer parts of large stems are of the so-called heterogeneous type II, the multiseriate rays having fusiform outlines with short uniseriate wings as seen in tangential sections (*Fig. 2*) and the low uniseriate rays being composed of upright cells. In young stems, e.g. twigs, the rays are of the heterogeneous type I and the first-formed multiseriate rays extend outward from the interfascicular parts of the eustele. The most conspicuous difference between the rays of *Euptelea* and those of *Trochodendron* and *Tetracentron* is the precocious and extensive sclerification of the multiseriate rays in the phloem of *Euptelea*.

NODAL ANATOMY AND LEAF

The nodal anatomy of *Euptelea* is distinctive of the genus and is of a type that has not been encountered by us in any other large woody dicotyledon. At the base of normally enlarged leaves of mature plants, there are 5–11 foliar vascular strands (*Figs. 3* and *6*), preliminary investigations indicating that such strands tend to be more numerous in *E. pleiosperma* than in *E. polyandra*. At certain levels of the attachment of the leaf (*Figs. 7* and *8*), these strands *commingle* with those of the axillary bud forming an arc of vascular strands that confronts a single broad parenchymatous region of the eustele. Thus, the node is of a much modified unilacunar type in which the vascular strands of the axillary bud extend [1] downward *between* the foliar strands of the leaf. In passing outward through the petiole, the foliar vascular strands first aggregate into an arc (*Fig. 4*) and subsequently into a vascular cylinder (*Fig. 5*) which extends into the midrib of the lamina.

The lamina of the leaf contains no branching idioblasts, either sclerotic or secretory, such as occur so characteristically in *Trochodendron* and *Tetracentron*. The epidermal cells surrounding the stomata are not of special form and orientation, and the stomatal apparatus as a whole bears no resemblance to the bizarre and highly modified stomatal structures of *Trochodendron*.

REPRODUCTIVE PARTS

The development of both the vegetative and the flower-bearing shoots of *Euptelea* is sympodial, no functional terminal buds being formed at the end of the growing season. This is in contrast to *Tetracentron* and *Trochodendron*, where extension of purely vegetative shoots is monopodial and that of flower-bearing ones is sympodial. The flower buds of *Euptelea* have numerous sterile scales which are succeeded on incipient shoots by 6–12 floriferous bracts and these subsequently by a varying number of leaves. The flowers are born singly in the axils of the floriferous bracts. The inflorescences of *Trochodendron* and *Tetracentron* are terminal, whereas the flower-bearing part of a fertile shoot of *Euptelea* is succeeded by a more or less extensive leaf-bearing prolongation. The fertile part of the shoot thus resembles the so-called intercalary inflorescences of *Drimys*, but in the latter genus monopodial extension of the axis does not terminate at the end of a growing season.

The flowers of *Euptelea* have long pedicels (*Fig. 9*), the apex of which flares into a disc-like receptacle devoid of perianth. A variable number of stamens are born in a whorl on the outer rim of this receptacle. At least in the case of specimens of *E. polyandra* growing at the Arnold Arboretum, the stamens are protandrous and caducous, stamen scars only (*st. sc.*, *Fig. 9*) being present at a stage when the enlarging carpels become receptive. The conspicuously stipitate carpels are likewise borne in a whorl. The vascular system of the flower is remarkably simple. A

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[1] The wording used in this paragraph is purely descriptive and bears no implications regarding developmental sequences.

eustele of many small strands extends throughout the pedicel. This eustele resolves at the base of the receptacle into a whorl of staminal traces, the remaining vascular tissue becoming carpellary strands, one to each carpel. There is no residual vascular tissue in the torus.

The microsporophyll of *Euptelea* is differentiated into a slender filament, an extensive connective, and an acuminate vascularized apex which projects above the thecae (*Fig. 13*). The four elongated and conspicuously protruding sporangia are laterally oriented in pairs. A single vascular strand extends throughout the microsporophyll, terminating at its apex. The endothecia may completely jacket the sporangia (*Figs. 14* and *15*) as in the Winteraceae. Occasionally they may extend across the adaxial side of the connective (*Fig. 14*).

The pollen grains are of two types, a tricolpate form which is characteristic of most specimens of *E. pleiosperma* and a polycolpate (mostly hexacolpate) one which predominates in a majority of the examined specimens of *E. polyandra*. However, one collection of *E. polyandra* (*Sawada*, April 9, 1927 [UC 382263]) has tricolpate pollen, and two collections of *E. pleiosperma* (*Forrest 16206* and *Wilson 1048*) have polycolpate grains. The grooves of the hexacolpate pollen are arranged in several patterns, two of the commonest of which are illustrated in *Figs. 16* and *17*. The reticulation of the exine (*Fig. 18*) is extremely fine, giving to the exine at times the appearance of being minutely pitted. The floor of the grooves is covered with small slightly embossed papillae which may be aggregated into chains. The contrast between the papillate and reticulate areas of the exine is slightly intensified in the drawing.

The megasporophylls (*Fig. 9*) have much elongated stipes and superficially resemble those of *Drimys stipitata* Vickery, except that the stigmatic surfaces of the conduplicate lamina do not protrude to form conspicuous double stigmatic crests as in the Winteraceae and Schisandraceae. The carpels, both during their earlier stages of development (*Fig. 10*) and at anthesis (*Figs. 11* and *12*), fluctuate markedly in external form. They are particularly significant from both developmental and phylogenetic points of view in illustrating successive morphological modifications in the closure of primitive conduplicate ranalian megasporophylls and in the restriction of their stigmatic surfaces. The stipe contains a single vascular strand which divides in the base of the conduplicate lamina (*Fig. 12*) into a dorsal vein and a strand which bifurcates just below the stigmatic level of the carpel into two ventral veins. The dorsal vein, which parallels the contour of the dorsal edge of the carpel, forms a conspicuous lateral branch which traverses the carpel above its locule and unites with the ventral veins (*Figs. 12* and *19*).

In addition to an over-all enlargement of the carpel to form the fruit, there is a marked elongation in the region below the stigmatic surfaces (compare *Figs. 12* and *19*). The fruit is papyraceous and contains 1–3 (rarely 4) small anatropous seeds (*Fig. 20*). The outer seed coat consists of an external layer of large thin-walled cells, which give a reticu-

late appearance to the seed, and an inner sclerenchymatous layer. The inner seed coat is composed of small thin-walled cells. There is an abundant endosperm in which is embedded a small embryo with incipient cotyledons. A foot-like structure composed of very small parenchymatous cells is located at the chalazal end of the endosperm and presumably is a structure derived from the antipodal cells of the megagametophyte.

DISCUSSION

Tetracentron and *Trochodendron* exhibit numerous morphological similarities, the *totality* of which provides convincing evidence of relatively close genetic relationship. Particularly significant in this connection are similar trends of morphological specialization of the vesselless xylem, the stomata, carpels, stamens, ovules, and seeds. None of these salient developmental and structural peculiarities occur in *Euptelea*.

The evolutionary gap between the vesselless xylem of *Trochodendron* and *Tetracentron* and the vessel-containing wood of *Euptelea* is so wide that it alone serves as a serious, if not insuperable, obstacle to the inclusion of *Euptelea* in the Trochodendraceae, and completely neutralizes any structural similarities between the rays and the wood parenchyma of the three genera. So-called heterogeneous type II rays occur in diverse families of dicotyledons which have attained comparable levels of parallel phylogenetic development and of themselves are not indicative necessarily of close genetic relationships. Furthermore, the precocious and extensive sclerification of multiseriate rays in the phloem of *Euptelea* — as in Winteraceae and certain other families of dicotyledons — is a type of structural specialization that does not occur in *Trochodendron* and *Tetracentron*. Nor is the occurrence of a high ratio of diagonal partitions in wood parenchyma strands, by itself, indicative necessarily of close genetic relationship, since such partitions occur for example in certain representatives of such remotely related families as the Magnoliaceae (sensu stricto) and the Saxifragaceae.

The extension of vegetative shoots of *Euptelea* is sympodial, whereas that of *Trochodendron* and *Tetracentron* is monopodial. The normally enlarged leaves of adult *Eupteleae* have unilacunar nodal attachments that are characteristically modified by peculiarities in the vascularization of the axillary buds. On the contrary, comparable leaves of *Tetracentron* and *Trochodendron* have trilacunar and multilacunar nodes and the vascularization of the axillary buds is of a commonly occurring and fundamentally different dicotyledonous type. The vascularization patterns of the petiole and lamina differ in the three genera, but such patterns should not be unduly emphasized in discussions of relationships, since they frequently fluctuate widely not only within the limits of specific genera and families but also in different leaves of a single plant. The stomata of *Euptelea* do not exhibit the peculiar structural specializations that occur so characteristically in *Trochodendron* and *Tetracentron*. Nor does *Euptelea* form branching idioblasts of either sclerotic or secretory types.

The inflorescences of *Trochodendron* and *Tetracentron* are truly terminal,

whereas the fertile part of the axis in *Euptelea* subtends a leaf-bearing terminus. The flowers of the two categories of genera differ markedly both in the external form and the internal structure of their constituent parts. The conspicuously stipitate, style-less carpels of *Euptelea* illustrate a distinct trend of specialization and closure of the primitive, open, conduplicate, ranalian megasporophyll which is entirely unlike that which has given rise to the style-bearing carpels and basally incipient syncarpy of *Trochodendron* and *Tetracentron*. Furthermore, the ovules of *Euptelea* do not have the vascularized subchalazal projection which is such a distinctive feature of the ovules of the latter genera. The fundamental differences in the carpels are reflected in the fruits, those of *Euptelea* being clusters of samaras and those of *Tetracentron* and *Trochodendron* being folliceta with ventral loculicidal dehiscence. The slender much elongated seeds of the latter genera have characteristic extensions of the vascularized subchalazal projections and resemble those of *Euptelea* only in characters, e.g. copious endosperm, small embryo, etc., which are indicative of general rather than of specific ranalian affinities.

The stamens of *Euptelea* differ from those of *Trochodendron* and *Tetracentron* not only in their external form but also in the development of their endothecia. They are attached to the rim of a flattened torus, whereas in *Trochodendron* the free parts of the filaments arise from the dorsal surfaces of the carpels. The pollen of *Euptelea* fluctuates from tricolpate to polycolpate, tricolpate grains tending to be dominant in *E. pleiosperma* and hexacolpate ones in *E. polyandra*. In *Tetracentron* and *Trochodendron*, the pollen grains are prevailingly tricolpate, are smaller than those of *Euptelea*, have narrower grooves, a more coarsely reticulate exine, and in *Trochodendron* a crestlike median thickening of the floor of the grooves. Tricolpate pollen having reticulate exines and papillate thickenings on the floor of the grooves occurs in various dicotyledons. Furthermore, transitions from tricolpate to polycolpate grains occur in Ranunculaceae, Berberidaceae, and in other families. Thus, the morphology of the pollen, by itself, is not indicative necessarily of close relationship between *Euptelea* and *Trochodendron* or *Tetracentron*.

The chromosomes of the two categories of genera differ in size, form, and number, the basic number in *Euptelea*, as in *Illicium* and the Schisandraceae, being 14, whereas in *Trochodendron* and *Tetracentron,* as in *Cercidiphyllum* and certain Magnoliaceae and Winteraceae, it is 19 (see Whitaker, 7).

The morphological differences between *Euptelea* and *Trochodendron* are numerous and indicative of divergent trends of phylogenetic specialization in all organs of these plants. Significant structural similarities are few and are suggestive of common ranalian ancestry rather than of actual close genetic relationship between the two genera. Why then should the genera have been placed in the same family? The decision to do so appears to have been based largely, if not entirely, upon the absence of a perianth, resulting in the inclusion of such strange bedfellows as *Eucommia, Cercidi-*

phyllum, Euptelea, and *Trochodendron* in the Trochodendraceae. *Eucommia* and *Cercidiphyllum* have subsequently been placed in separate unigeneric families, and we agree with van Tieghem (6) and Smith (5) that *Euptelea* should similarly be placed in an independent family, the Eupteleaceae.

As in the case of the Winteraceae (see Bailey and Nast, 1), the family Eupteleaceae exhibits evidences of general ranalian affinities, but does not appear to be closely related to any specific surviving family of the ranalian complex. It obviously cannot be placed in close proximity to those woody ranalian families (see Bailey and Nast, 2), which are characterized by having monocolpate and derived types of pollen and numerous aromatic secretory cells. Although it appears to belong in the category of ranalian families having tricolpate and derived types of pollen and no aromatic secretory cells, it cannot be placed in close proximity to any of them, e.g. Ranunculaceae, Berberidaceae, Lardizabalaceae, Menispermaceae, or Trochodendraceae. It remains to be determined whether the family Cercidiphyllaceae is of ranalian rather than of rosalian affinities, but in any case it is not closely related to the Eupteleaceae. Nor does the latter family form a natural compact grouping with the Schisandraceae.

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EXPLANATION OF PLATES

Plate I

Fig. 1. *Euptelea polyandra.* Transverse section of the wood, × 120. Fig. 2. The same. Tangential longitudinal section of the wood, × 120.

Plate II

Fig. 3. *Euptelea polyandra.* Transverse section of lower part of petiole, × 20. Fig. 4. The same. Transverse section of middle part of petiole, × 20. Fig. 5. The same. Transverse section of upper part of petiole, × 20.

Plate III

Figs. 6–8. *Euptelea polyandra.* Transverse sections of node, showing vascular strands of leaf and bud, approx. × 16. Fig. 9. *E. pleiosperma, Forrest 25460.* Flower, showing mature carpels after stamens have fallen. Stamen scar, *st. sc.,* approx. × 6½. Fig. 10. The same, *Hers 930.* Young carpel, approx. × 77. Fig. 11. *E. polyandra, Wilson 6704.* Mature carpel, approx. × 13. Fig. 12. *E. pleiosperma, Forrest 25460.* Mature carpel. Dorsal bundle, *d. b.;* dorsal branch, *d. br.,* approx. × 10.

Plate IV

Fig. 13. *E. pleiosperma, A.A. 14796* (cult.). Stamen showing extension of sporophyll above the thecae, × 15. Fig. 14. *E. polyandra, A.A. 865* (cult.). Transverse section of stamen, × 825. Fig. 15. *E. pleiosperma, A.A. 14796* (cult.). Transverse section of stamen, × 825. Figs. 16, 17. *E. polyandra.* Hexacolpate pollen grains showing position of grooves. Fig. 18. *E. pleiosperma, Feng 621.* Tricolpate pollen grain, × 7500. Fig. 19. *E. pleiosperma, Tsai 63095.* Fruit, approx. × 4½. Fig. 20. The same. Seed, approx. × 12½.

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